Translocation of potassium and phosphate from ordinary and proteoid roots to shoots in the Proteaceae

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Investigation of potassium and phosphate uptake, using intact plants, showed an accumulation of these elements in proteoid roots, while translocation occurred more readily from ordinary roots. These results, as well as auto-radiographic studies, indicated that proteoid roots may act as sinks. The presence of sucrose in the experimental solution stimulated the translocation of phosphate from the proteoid roots. The inhibition of phosphate translocation by the respiratory uncoupler, 2,4-dinitrophenol (DNP) seems to be evidence for the involvement of an energy dependent mechanism or mechanisms in the translocation of ions from proteoid roots to the aerial parts of the plant.
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Die bestudering van kalium- en fosfaatopname met intakte plante het aangetoon dat ophoping van hierdie elemente in proteoïede wortels plaasvind, terwyl dit meer geredelik vanuit gewone wortels na die bogrondse dele vervoer word. Hierdie bevindings, sowel as dié verkry tydens outo-radiografiese ondersoeke, dui daarop dat proteoïede wortels as 'n ophopingsgebied ('sink') vir ione dien. Die teenwoordigheid van sukrose in die eksperimentele oplossing bevorder die vervoer van fosfaat vanuit proteoïede wortels. Die onderdrukking van die vervoer deur die respiratoriese ontkoppelaar, 2,4-dinitrofenol (DNP), dui moontlik daarop dat 'n energie-afhanklike meganisme of meganismes in die vervoer van ione vanuit proteoïede wortels na die bogrondse dele betrokke is.
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Introduction

In previous work on potassium and phosphate absorption by ordinary and proteoid roots of the Proteaceae, excised tissues were used (Vorster & Jooste 1986). Since results obtained with excised plant material cannot unconditionally be applied to the whole plant (Lüttge & Higinbotham 1979), the uptake and transport capacities of ordinary and proteoid roots, using intact plants, were investigated.

Materials and Methods

Leucadendron uliginosum R.Br. plants (8 to 12 months old), obtained from nurseries, were used. Plants of comparable size were selected, the roots washed in running tap water, rinsed in deionized water, and subsequently placed in an aerated 0,5 mmol dm^{-3} $CaSO_4$ solution.

Plants were divided into two groups. For absorption by proteoid roots, clusters were immersed separately, but still intact, in the experimental solution. For ordinary roots, a group of roots was placed in the same way in the experimental solution. Figure 1 illustrates the apparatus and the method according to which either the ordinary or the proteoid roots were subjected to absorption of the particular element.

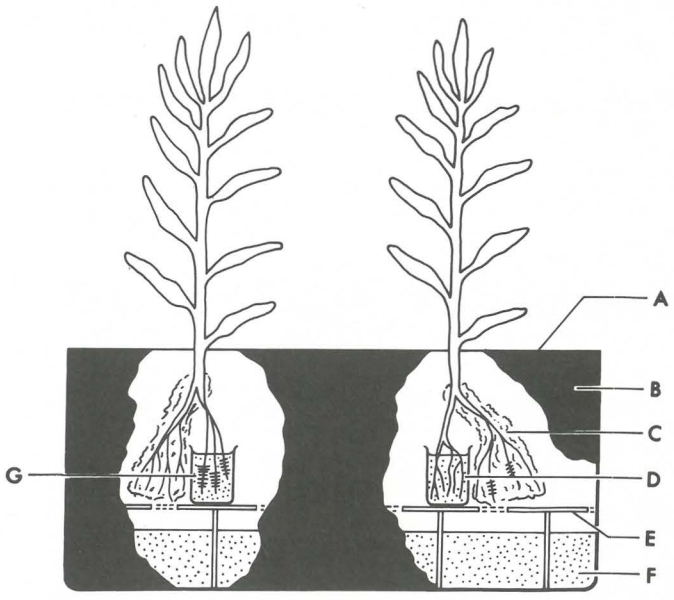

Figure 1 Experimental design to expose intact ordinary or proteoid roots to labelled elements. A. Plastic covering; B. Black paper covering; C. Moistened absorbent paper; D. Ordinary roots exposed to experimental solution; E. Grid; F. Water; G. Proteoid roots exposed to experimental solution.

A large rectangular glass container (300 × 300 × 400 mm) was covered with black paper to avoid exposure of the roots to light. A stainless steel grid was placed at a height of approximately 120 mm from the bottom of the container on which the beakers, containing the experimental solutions, were placed. The container was subsequently filled with water to a level just below the grid to provide a humid atmosphere to the roots not exposed to the experimental solution. Possible desiccation of these roots was further prevented by covering them with moistened absorbent paper. Finally the container was covered with black plastic material.

The roots were exposed to the experimental solution for 24 h, excised, the excess solution was removed by blotting, and the fresh mass determined. The aerial parts were removed and dried in a plant press at 80°C for 12 h. The dried parts were divided into segments (of uniform length in each experiment; segment one just above the root system), and ground separately. Samples of known mass were dry ashed according to an adaptation of the method described by Du Preez *et al.* (1981) and analysed radiometrically by liquid scintillation counting using a commercial scintillation mixture. Potassium and phosphate uptake were calculated from the ^{86}Rb and ^{32}P content of the samples and the specific activity of the experimental solutions, and expressed as μg K (or P) g^{-1} (dry mass of aerial parts) g^{-1} (fresh mass of roots exposed to the experimental solution).

The experimental solutions contained KCl or KH_2PO_4 at a concentration of 0,5 mmol dm^{-3} in a 0,5 mmol dm^{-3} $CaSO_4$ solution, while ^{86}Rb as substitute for ^{42}K (Epstein & Hagen 1952; Epstein 1961; Rains *et al.* 1964) or ^{32}P (both obtained from the Radiochemical Centre, Amersham, U.K.) were added as tracers. Approximately 83,25 kBq per 500 cm^3 experimental solution were used. Amounts of 60 cm^3 of the experimental solutions in 80 cm^3 beakers were used for exposure of the roots.

In the experiments on the effect of sucrose on the translocation of phosphate from proteoid and ordinary roots, the experimental solution contained 200 mmol dm^{-3} sucrose.

In the experiments on the effect of sucrose vs. sucrose plus 2,4-dinitrophenol (DNP) on translocation, only proteoid roots were exposed to the experimental solutions. Furthermore, all the experimental plants in this experiment were previously exposed to a labelled 0,5 mmol dm^{-3} KH_2PO_4 solution (the 'first' solution) for 1 h to ensure absorption of the labelled element — known as a period of pre-loading (Epstein 1972). Hereafter the plants were removed from the first solution and placed in the next experimental solution (the 'second' solution) for a period of 24 h. The second solution was of the same composition as the first solution, but also contained 200 mmol dm^{-3} sucrose, and the tracer was omitted. Half of the series of second solutions contained DNP at a concentration of 0,5 mmol dm^{-3}.

For the autoradiographic investigation, the roots of the plants were rinsed and temporarily placed in an aerated 0,5 mmol dm^{-3} $CaSO_4$ solution at 25°C. The plants were then placed in an aerated experimental solution (500 cm^3) at 25°C for 80 min so that only the roots were covered. The experimental solution contained 0,5 mmol dm^{-3} KH_2PO_4. As in the previous experiments, ^{32}P (166,5 kBq per 500 cm^3) was used as tracer.

Three to four replicates of each treatment were employed; each experiment was repeated at least twice on consecutive days. The mean and standard error for each treatment were calculated. Differences between means of more than twice the standard error were regarded as significant.

Results and Discussion

Translocation of potassium and phosphate from ordinary and proteoid roots to the shoot

The results presented in Tables 1 and 2 might appear to be contradictory to previous findings, namely that proteoid roots are characterized by a higher absorption capacity than ordinary roots (Vorster & Jooste 1986). Repeated execution of the experiment confirmed that the elements concerned are translocated much more effectively from the ordinary roots than from the proteiod roots to the aerial parts. Approximately 278 and 168% more potassium and phosphate respectively were translocated from the ordinary than from the proteoid roots to the shoot.

This observation could have been influenced by the initial potassium and phosphate status of the roots. If it is assumed that the proteoid roots initially had a higher internal potassium and phosphate content than ordinary roots, and that the incoming label equilibrates at least partially with the internal pools of potassium and phosphate, this could cause a differential isotopic dilution of the incoming label, with the effect that label entering proteoid roots becomes more heavily diluted (internal label has a lower specific activity in proteoid roots). Consequently a greater amount of label could have been present in the shoots of plants to which potassium and phosphate were supplied to the ordinary roots.

In view of previous work (Vorster & Jooste 1986) a significantly higher initial potassium and phosphate content of proteoid roots seems unlikely, and proteoid roots probably serve as a temporary sink. This possibility was also suggested by Jeffrey (1967), Gardner *et al.* (1981), and Specht (pers. comm.).

Table 1 Uptake (± standard error) and distribution of potassium in shoots following exposure of ordinary and proteoid roots to a 0,5 mmol dm^{-3} KCl solution

	K uptake[a]	
Shoot segments	Proteoid roots exposed	Ordinary roots exposed
1	12,15 ± 2,85	52,63 ± 6,28
2	2,84 ± 0,48	8,31 ± 0,79
3	1,36 ± 0,48	4,02 ± 0,89
4	1,80 ± 0,23	3,59 ± 0,91

[a] μg K g^{-1} (dry mass of aerial parts) g^{-1} (fresh mass of exposed roots)

Table 2 Uptake (± standard error) and distribution of phosphate in shoots following exposure of ordinary and proteoid roots to a 0,5 mmol dm^{-3} KH_2PO_4 solution

	P uptake[a]	
Shoot segments	Proteoid roots exposed	Ordinary roots exposed
1	35,0 ± 12,15	72,8 ± 17,38
2	26,8 ± 8,21	79,3 ± 19,82
3	23,6 ± 7,61	86,1 ± 11,00
4	25,2 ± 9,66	74,0 ± 17,31
5	31,1 ± 8,50	63,0 ± 12,08
6	10,1 ± 3,74	31,4 ± 7,68

[a] μg P g^{-1} (dry mass of aerial parts) g^{-1} (fresh mass of exposed roots)

Autoradiographic investigation

In view of the above findings, it was decided to try to gain more insight into the uptake by and translocation from ordinary and proteoid roots by means of an autoradiographic investigation.

Figure 2 clearly shows an accumulation of ^{32}P in the proteoid roots. Even where the ordinary roots show a dense cluster on the photograph the activity is not as high as in the proteoid roots.

These results further support the assumption that the proteoid roots accumulate phosphate while it is more readily translocated from ordinary roots to the shoot.

The effect of sucrose on the translocation of phosphate from ordinary and proteoid roots to the shoot

In view of previous findings showing that proteoid roots possess a greater capacity for metabolic absorption than ordinary roots (Vorster & Jooste 1986), the possibility exists that the lack of a source of sufficient energy may restrict translocation to the aerial parts of the plant.

It was found that sucrose was essential in the ambient solution to maintain continuous xylem sap exudation in excised maize roots (Jooste unpublished data). Gorham (pers. comm.) confirmed this finding. In view of this it was decided to establish whether the presence of sucrose in the experimental solution influences the translocation of ions from proteoid and ordinary roots to the shoot.

In the absence of sucrose (Table 2), about 168% more phosphate was translocated from ordinary roots than from proteoid roots. In contrast to this, in the presence of sucrose (Table 3), in total approximately 18% more phosphate was translocated from proteoid than from ordinary roots to the aerial parts of the plants.

From these results it is clear that sucrose must have contributed to the translocation of phosphate from the proteoid roots. It is possible that an energy dependent mechanism, or mechanisms, might be involved in the translocation of ions from proteoid roots to the shoot.

The effect of sucrose versus sucrose plus DNP on the translocation of phosphate from proteoid roots to the shoot

In view of the enhanced ion translocation by proteoid roots in the presence of sucrose, the possible involvement of an energy yielding process might be suspected. Eliminating such a process by addition of DNP, a respiratory uncoupler, would thus shed additional light on this phenomenon. Results obtained in this experiment are presented in Table 4.

Table 3 Uptake (± standard error) and distribution of phosphate in shoots following exposure of ordinary and proteoid roots to a 0,5 mmol dm^{-3} KH_2PO_4 solution plus sucrose

	P uptake[a]	
Shoot segments	Proteoid roots exposed	Ordinary roots exposed
1	81,12 ± 10,92	64,76 ± 12,42
2	21,64 ± 3,70	25,45 ± 9,47
3	13,62 ± 6,97	7,89 ± 3,06
4	7,05 ± 5,36	6,11 ± 3,29

[a] $\mu g\ P\ g^{-1}$ (dry mass of aerial parts) g^{-1} (fresh mass of exposed roots)

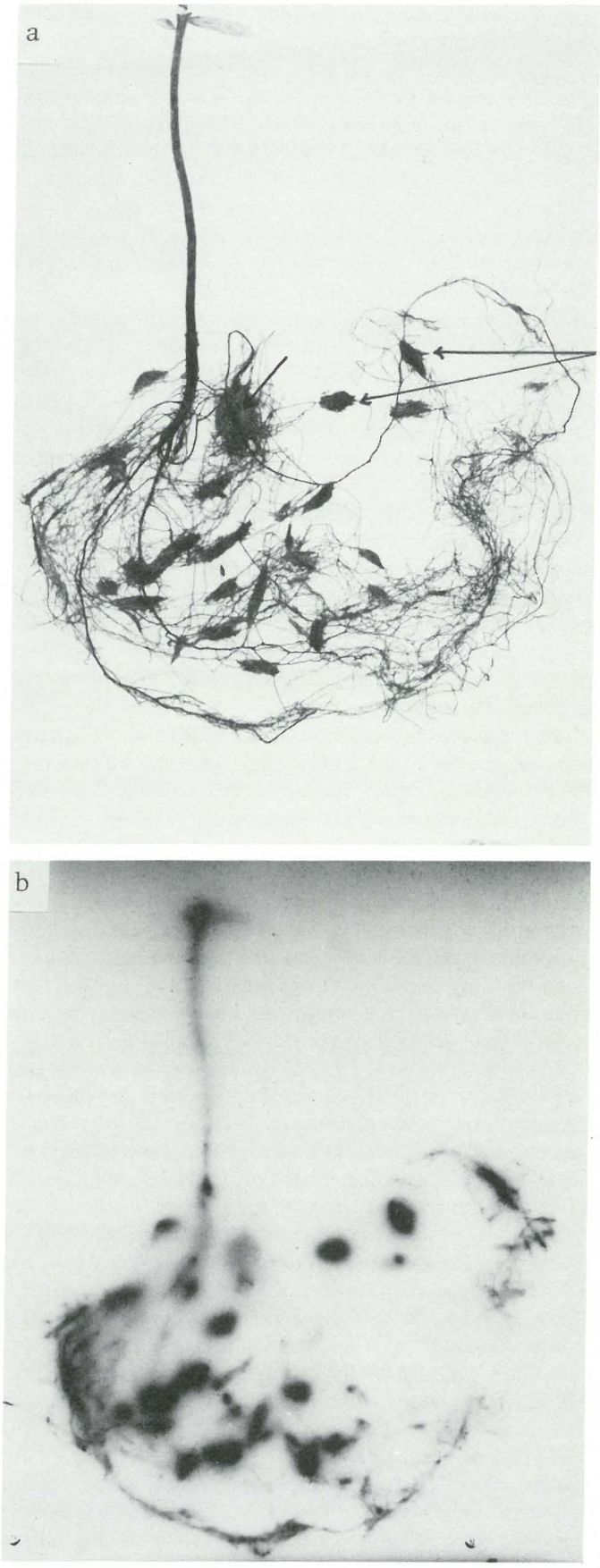

Figure 2 Photograph (a) and autoradiograph (b) of root system following exposure to a labelled 0,5 mmol dm^{-3} KH_2PO_4 solution. (Arrows indicate proteoid roots.)

DNP inhibited phosphate translocation to the shoot by approximately 80%, presumably by suppressing ATP-synthesis, making less energy available for the translocation of phosphate to the aerial parts of the plants.

Table 4 Uptake (± standard error) and distribution of phosphate in shoots following exposure of proteoid roots to a 0,5 mmol dm^{-3} KH_2PO_4 solution (plus sucrose) with and without DNP

Shoot segments	P uptake[a]	
	With DNP	Without DNP
1	4,32 ± 2,56	28,47 ± 5,55
2	2,03 ± 2,48	5,81 ± 1,93
3	1,57 ± 1,92	3,67 ± 4,64
4	0,62 ± 0,19	1,68 ± 0,67

[a]µg P g^{-1} (dry mass of aerial parts) g^{-1} (fresh mass of exposed roots)

The amount of potassium (Table 1) and phosphate (Tables 2,3 & 4) in the different shoot segments show that both elements are quite readily distributed throughout the aerial parts of the plants.

Acknowledgements

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